

pose any way of measuring accurately such a transmitter/receiver ratio; nor indicate how such a measure might elucidate the kinds of culture change with which anthropologists and historians have to deal.

Further, if we attempt to translate the transmitter/receiver ratio into terms that may be more familiar to social scientists (by equating receivers with initiates and transmitters with elders, without regard to any cultural complexities such as occupational specialization), much of what they seem to be indicating is that a bottom-heavy demographic pyramid leads to rapid cultural change. The view that population pressure as such ordinarily leads to technological innovation, and thus cultural change, has in fact been expounded with considerable skill and erudition, and with appropriate data, by social scientists<sup>16,19,27-31</sup>.

\* Darwin, following Malthus, focused upon the constraining features of the environment in the face of expanding population size as leading to intra-specific competition, and consequently (to Darwin) natural selection. Humans, however, in the face of demographic pressure, can technologically alter the relationship between society and environment. The effect is to mitigate the Malthusian 'struggle for existence', and Darwin's appropriation of it, as a necessary condition for selection.

It is a notable irony that this approach is explicitly anti-Malthusian, and consequently anti-Darwinian!\*

Biological parallels to cultural evolution have, in fact, been proposed before, though usually with candid acknowledgement of their limitations<sup>32-36</sup>. It remains, however, that these biological models are but metaphors, and of no greater applicability *a priori* to cultural processes than are quantum mechanics or the full-court press. Moreover, few of these biological models have been tested, and none appears to be capable of dealing with such fundamental cultural processes as the rise or collapse of civilizations<sup>37</sup>. Finally, if culture 'evolves' then it is an analogue of the gene pool and the property of a society (as a gene pool is the property of a population); yet, if culture is transmitted and possessed by individuals, it is an analogue of the genotype. Muddling the fundamentals of this analogy effectively precludes its rigorous application. □

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## Macroevolution

# Large-scale replacements in the history of life

from Michael J. Benton

THE great debate over whether evolution proceeds gradually or in jumps highlights only one area of evolutionary biology where major changes in thinking are taking place. Studies of evolution at the next higher level — the search for underlying pattern in, and explanations for, the replacements of whole families, orders or classes over geological time — have also yielded exciting results. New analyses suggest that the classical view, that some groups die out simply because they become 'out of date' and are replaced by their more efficient competitors over long periods of time, is not an adequate explanation. There is increasing evidence that major physical changes have caused more large-scale evolutionary changes than has competition. At the same time, computer simulations suggest that the apparent pattern in disappearances of whole groups may sometimes be the result of a purely random summing of events at a lower level.

Worldwide replacements of major taxonomic groups have occurred many times during the history of life and palaeontologists have typically sought particular reasons for each extinction event. Such deterministic explanations include both large-scale 'competition' and extinction followed by a new adaptive radiation. Competition at the individual level, or differential survival at the species level, has been the favoured explanation when two taxonomic groups that

apparently occupy the same broad adaptive zone coexist for some time and one increases in abundance at the expense of the other. The alternative view, that certain major changes in the history of life are to be ascribed to changes in the physical environment, is particularly applied to mass extinction events that are followed by adaptive radiations of other groups. These two kinds of explanation rely respectively on biological effects ('competition') and physical effects (causing mass extinction) and of course the two are inseparable in the environment of any species.

A third viewpoint has been advanced that all change at higher taxonomic levels in the history of life is random. Species evolve and become extinct at random, and a set of chance extinctions may lead to the extinction of a whole larger group. The idea has been tested by running computer simulations of evolution, and the random patterns that result are very similar to the patterns of evolution as recorded in the fossil record<sup>1</sup>. However, a dissenting viewpoint is that at certain times, for example during adaptive radiations and mass extinctions, there are identifiable causes<sup>2</sup>. For example, during an adaptive radiation the probability of speciation may be enhanced by the acquisition of a new adaptive innovation.

From a theoretical viewpoint, we can suggest three models for large-scale extinction/replacement events: (1) com-

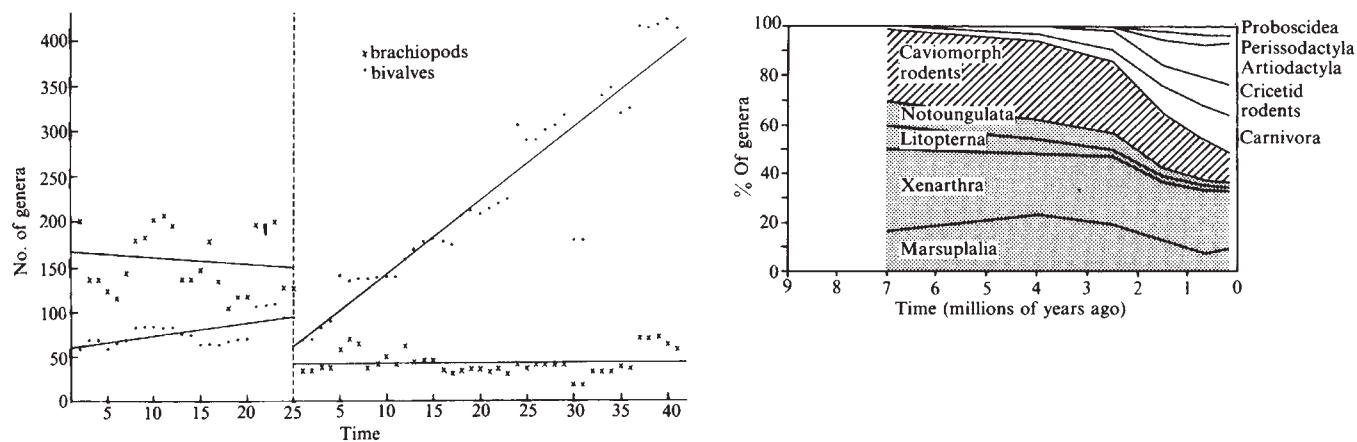
petition/differential survival (biological factors): numerous competitive encounters between individuals or species in which those belonging to one lineage have a constantly higher probability of survival; (2) mass extinction/opportunistic replacement (physical factors): all members of a particular lineage become extinct at the same time and are replaced by another lineage after the extinction; (3) stochastic (random): a mixture of biological and physical factors; at the level of individuals or species, each death/extinction has a particular cause, but the sum is random with respect to the whole lineage.

'Competitive' explanations have traditionally been used by palaeontologists to account for the replacement of brachiopods by bivalves, the replacement of mammal-like reptiles by dinosaurs, the partial replacement of perissodactyls by artiodactyls and the success of North American mammals in South America. In all cases, these explanations have been questioned by a closer study of the fossil record.

Gould and Calloway<sup>3</sup> plotted the numbers of genera of brachiopods and bivalves against time and demonstrated that the major extinction events at the end of the Permian (225 Myr) reduced brachiopod numbers more drastically than those of the bivalves. The latter group recovered and radiated rapidly while the brachiopods maintained the same low diversity ever after (Fig. 1). The crucial blow was the extinction event (external physical causes) and not gradual competitive attrition of one group by the other.

The same conclusion seems to hold for the replacement of mammal-like reptiles by thecodontians, and then by their descendants, the dinosaurs, during the Triassic Period (225–190 Myr). A gradual competitive model has also been traditionally assumed, with dinosaur success ascribed to supposedly superior locomotory, feeding or thermoregulatory ability. Plots of numbers of species, or of individual animals, against time show, however, that the carnivorous thecodontians remained unimportant throughout the Triassic and failed to replace their competitors, the cynodont mammal-like reptiles. The dinosaurs radiated rapidly towards the end of the Period, after the extinction of the groups they replaced<sup>4</sup>.

During the Tertiary, the artiodactyls (cattle, antelopes, camels and so on) largely replaced the perissodactyls (horses, rhinos, numerous extinct groups) and this has been explained in terms of the competitive advantage of various characters of their limbs and teeth and the ability to ruminate. Now, however, Cifelli<sup>5</sup> has found no relationship between the relative diversities of both groups through time, and no evidence of competition or ordinal displacement.



**Fig. 1** (above left) Numbers of brachiopod genera and bivalve genera plotted against time. The time units correspond to geological stages and their length varies from about 5 to 10 Myr each. The vertical dashed line marks the Permo-Triassic boundary: the diversity of both groups was much reduced, but the bivalves recovered and radiated thereafter. The success of bivalves was probably not the result of continued attritive competition with the brachiopods. From ref. 3. **Fig. 2** (above right) Percentages of genera of different groups of mammals in South America over time. The shaded groups are endemic to South America, and the unshaded groups are typical of North America. The Panamanian land-bridge opened 3 Myr ago and North American invaders appear to have competed successfully with some of the typical South American natives. However, environmental changes caused many of the replacements. From ref. 9.

The most cited, and most studied, example supposedly indicating competitive replacement is the 'great American interchange'. Three million years ago, the Panamanian land-bridge appeared and permitted the previously isolated faunas of North and South America to intermingle<sup>6-9</sup>. Many native South American genera of mammals became extinct and were replaced by a slightly larger number of North American genera (Fig. 2). Certain South American groups (for example, Notoungulata, Litopterna, Xenarthra: large herbivores) were little affected, however, and North American invaders insinuated themselves into the faunas without causing extinctions. Environmental and climatic changes also tended to favour some North American groups. In addition, many South American mammals moved north and successfully established themselves in Central and North America. There is no clear evidence of the constant competitive superiority of one group over another.

A possible case of ongoing competitive replacement has been studied by Stanley and Newman<sup>10,11</sup>. Balanoid barnacles compete successfully with chthamaloid barnacles on the rocky coasts of parts of northeastern Europe where their ranges overlap. The balanoids are also currently undergoing a broad adaptive radiation, while the chthamaloids are apparently on the decline, and the success of the balanoids is ascribed to their advanced wall structure and feeding mechanism. The fossil record is, however, poor and it cannot be demonstrated that there has been a reciprocal radiation of balanoids and decline of chthamaloids over time, and the relative present-day success of the two groups may be explained by selective predation<sup>12</sup>. The evidence for competition as a major factor in this large-scale replacement is stronger than in most other cited examples, but it probably plays a

smaller part in the history of life than has been assumed.

Extinctions of large groups caused by physical factors and subsequent adaptive radiations can be seen in many cases in the fossil record. Further, it has become evident that there have been periods in the history of life during which numerous unrelated groups of plants and animals became extinct, apparently at the same time, and were replaced by new stocks. Among marine groups there have been four major extinction events<sup>13</sup>, during one of which, at the Permian-Triassic boundary, 225 Myr, over 90 per cent of shallow-water species died out. This has been explained by the reduction in continental shelf seas as the continents drifted together and fused into a single large land mass<sup>14</sup>.

Another major marine extinction event occurred at the Cretaceous-Tertiary boundary, 65 Myr, but this event is better known for the extinction of the dinosaurs and subsequent radiation of the mammals. Many hundreds of pages have been written about how the dinosaurs became extinct without our being any the wiser<sup>15-20</sup>. As with all extinction and replacement events, the pattern must be established before the process can be determined. Questions still to be answered about the extinction of the dinosaurs include: how long did it take; did it occur at the same time everywhere; were dinosaurs already in decline; did dinosaurs become extinct at the same time as the profound extinctions amongst marine plankton; to what extent did climatic, or other, changes increase the relative fitness of the mammals; and was competition involved?

Explanations of purely 'competitive' replacements and of opportunistic adaptive radiations after major extinctions are deterministic. They assign relative fitness values to different groups in order to explain selective survival or extinction in

the face of changes in either the biotic or the physical environment. The alternative stochastic approach is probably applicable to many major replacements<sup>21,22</sup>. In such cases, there is no single cause for the extinction but a whole range, including physical and biological factors, one or more for each species involved. Such explanations are probably valid more often than has been assumed, although they may seem unsatisfactory — an admission of no definite conclusion. They include, however, all cases between purely competitive take-overs and major extinction/opportunistic replacement events. Competition may increase the probability of extinction of a particular lineage, but it will rarely be the sole cause, whereas it could be postulated that a catastrophic change in the physical environment is sufficient on its own. □

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